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NOTES AND INSIGHTS

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Ant-mediated seed dispersal in the Poaceae: Evidence of myrmecochory in green foxtail (*Setaria viridis*) and giant foxtail (*Setaria faberi*)

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Abstract

Ant-mediated seed dispersal is an expression of mutualism between plants and insects that may drive the diversification of flowering plants. However, despite its ecological and evolutionary importance, research on myrmecochory has lacked a tractable model system. Here, we studied seed dispersal in *Setaria viridis* and *Setaria faberi* (Poaceae) by ants. In field investigations, the caryopses of *S. viridis* and *S. faberi* were transported by *Tetramorium tsushimae* or *Formica japonica* workers. In the laboratory, *T. tsushimae* only removed the pericarp of *S. viridis*, leaving the rest of the seed intact, suggesting that the pericarp of *S. viridis* functions as an elaiosome. In contrast, *T. tsushimae* left the pericarp of all *S. faberi* seeds untouched. The presence of lipids in the pericarp of *S. viridis* and *S. faberi* was confirmed by Sudan IV staining. Overall, our findings provide the first experimental evidence of ant-mediated seed dispersal in *S. viridis* and *S. faberi*, demonstrating the occurrence of myrmecochory in the Poaceae. Because *S. viridis* offers rich genomic resources and is experimentally tractable, it has strong potential as a new model system.

KEYWORDS

diversification, elaiosome, mutualism, myrmecochory, predation

1 | INTRODUCTION

Mutualistic interactions have been found in many flowering plant taxa and are considered to contribute to plant diversification (Del-Claro & Torezan-Silingardi, 2021; Regal, 1977; Yamawo & Ohno, 2024). Seed dispersal between plants and animals is a ubiquitous mutualistic interaction in terrestrial ecosystems (Del-Claro & Torezan-Silingardi, 2021; Yamawo & Ohno, 2024). Ant-mediated seed dispersal, referred to as myrmecochory, is one of the most common mechanisms of animal-mediated seed dispersal and occurs across a wide variety of plant groups, including approximately 11 000 plant species spanning 334 genera (Berg, 1975; Lengyel et al., 2010; Nakanishi, 1988; Ohkawara et al., 1996). Ant-dispersed fruits or seeds typically possess an oily appendage, called the elaiosome, containing chemical substances that attract ants (Hughes et al., 1994; Pfeiffer et al., 2010) that carry the seed to their nest, consume the elaiosome, and abandon the undamaged seed either outside or within the nest, thereby dispersing it (Handel & Beattie, 1990). Some studies have indicated that

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myrmecochory is highly beneficial to plants, because it limits intraspecific competition (Kjellsson, 1991; Tanaka & Tokuda, 2016) and post-dispersal seed predation (Manzaneda & Rey, 2009; Tanaka et al., 2015), while directing the dispersal of seeds to suitable habitats (Gibson, 1993; Hanzawa et al., 1988). Comparisons of diversification rates between myrmecochorous and non-myrmecochorous lineages across multiple clades strongly suggest that myrmecochory contributes to increased diversification (Lengyel et al., 2009). However, to more rigorously evaluate the effect of ant–plant seed dispersal mutualism on plant diversification, it is essential to establish model systems with well-characterized genetic backgrounds. The Poaceae represent one of the most diverse plant lineages, and the identification of ant–seed dispersal mutualism within this family, together with the establishment of model systems, offers an opportunity to elucidate the specific processes through which such mutualism has driven plant diversification.

Setaria viridis (L.) P. Beauv. and *Setaria faberi* Herrm. (Poaceae) are annual grasses that grow in grasslands worldwide (Dekker, 2003). In Japan they are distributed on Hokkaido, Honshu, Shikoku, and Kyushu. *Setaria viridis* has gained attention as a model system for evolutionary biology (Dekker, 2004) and population genetics studies (Huang et al., 2014). It is locally adapted to various habitats such as shorelines and coastal habitats (Itoh et al., 2024). On the basis of our occasional observations of ants visiting the caryopses of these species, we predicted that these species would rely on ants for seed dispersal. Identifying the seed dispersal mechanisms in this group would also help establish model systems to study how ant–plant seed dispersal mutualism affects plant diversification.

2 | MATERIALS AND METHODS

2.1 | Field investigation

We conducted surveys to identify ant species that transport the caryopses of *S. viridis* and *S. faberi*. Fieldwork was carried out during the species' natural seed dispersal seasons: in July 2015 at Tomita-cho (40°58′80″ N, 140°47′90″ E), in July 2019 at Hirosaki University (40°58′81″ N, 140°47′38″ E), in Hirosaki City, northern Japan, and in August 2024 at the Center for Ecological Research, Kyoto University (CER) (34°97′12″ N, 135°95′75″ E), in Otsu City, central Japan (Table 1). These sites were randomly selected to be located at least 500 m from each other, with similar environmental conditions such as light availability and moisture. The vegetation of these grasslands was primarily composed of annual and perennial herbaceous species, including *Trifolium repens* (Fabaceae), *S. viridis*, *S. faberi*, and *Artemisia princeps* (Asteraceae). All of these study sites were dominated by *Formica japonica* (Formicinae) and *Tetramorium tsushimae* Emery (Myrmicinae).

TABLE 1 Survey sites and periods of observation of *Setaria viridis* and *Setaria faberi*.

Site	Coordinates	Survey period
Tomita-cho, Hirosaki City, northern Japan	40°58′80″ N, 140°47′90″ E	July 2015
Hirosaki University, Hirosaki City, northern Japan	40°58′81″ N, 140°47′38″ E	July 2019
Center for Ecological Research (CER), Kyoto University, Otsu City, central Japan	34°97′12″ N, 135°95′75″ E	August 2024

At each site, we observed ant activity and recorded which species carried the caryopses of the two species. Five to nine reproductive plants, each at least 1 m apart, were haphazardly selected from each study site. Ten caryopses per maternal plant were collected and placed on filter paper (2.5 cm × 2.5 cm) under the maternal plant. We used the interval programming function of a waterproof digital camera (WG-4, Richo, Tokyo) under each maternal plant and monitored the species of animals removing seeds and their numbers. The cameras were set to automatic exposures at 1-min intervals for 8 h from 09:00 on a sunny day.

2.2 | Laboratory experiment

To ascertain whether caryopsis removal by ants here qualifies as myrmecochory, we offered caryopses to two queen-right colonies (>500 workers) of *T. tsushimae* maintained in our laboratory. The colonies had been collected from the Hirosaki University campus in April 2015 and maintained on 10% sugar water and a few mealworms provided once a week. No special treatments, such as starvation, were applied before the experiments. Mealworms were not supplied on the experimental days. All seeds used in the experiments were collected from 10 individuals each of *S. viridis* and *S. faberi* at Hirosaki University and were used immediately after collection. Thirty caryopses of each species were individually placed ~5 cm from the nest entrance every 24 h, then 15 of each species were offered sequentially to each ant colony.

To confirm the function of the pericarp in seed dispersal mediated by *S. viridis* and *S. faberi*, we removed the pericarp from 30 caryopses with a knife and

compared the seed removal rate by *T. tsushimae* ant colonies with that of 30 intact caryopses as previously described. Intact caryopses from which the pericarp was removed were individually offered to the ants, ~5 cm from the nest entrance, with 15 caryopses of each species offered sequentially to each colony.

2.3 | Sudan IV test

We stained mature seeds obtained from herbarium specimens with Sudan IV to test for the presence of oils in the pericarp (Pearse, 1985). The pericarps were hand-sectioned transversely and treated with Sudan IV.

3 | RESULTS

Tetramorium tsushimae carried caryopses of *S. viridis* at all study sites (Figure 1), removing 92% (46/50) at Tomita-cho, 80% (40/50) at the CER, and 64.3% (45/70) at Hirosaki University (Figure 1). Dispersal distances averaged 37.6 ± 20.7 cm (mean ± SD, $n = 46$).

Tetramorium tsushimae carried fewer *S. faberi* caryopses, removing 24% (12/50) at Tomita-cho, 12% (6/50) at the CER, and 24.4% (22/90) at Hirosaki University (apart from two removed by *F. japonica* (Formicinae)). Dispersal distances averaged 14.4 ± 11.6 cm ($n = 12$).

When 30 caryopses of each species were individually laid out ~5 cm from the nest entrance in the laboratory, the ant workers immediately brought all caryopses of *S. viridis* into the nest but only three of *S. faberi*. Furthermore, only the pericarp of *S. viridis* caryopses was consumed after a few days; intact caryopses of *S. faberi* were discarded outside the nest (Figure 2). The removal of pericarp from *S. viridis* caryopses significantly reduced the rate of removal by ants (control, 80%; treatment, 20%; Fisher's exact test, $p < 0.001$). Sudan IV staining revealed the presence of oils at the base of the pericarp in both species (Figure 3).



FIGURE 1 Worker of *Tetramorium tsushimae* carrying a seed of *Setaria viridis*.

4 | DISCUSSION

Multiple field observations conducted across different populations and years revealed that caryopses of *S. viridis* are frequently removed by ants. Laboratory experiments supported these findings, showing that only the pericarp of *S. viridis* was consumed after a few days, while intact seeds were discarded outside the nest (Figure 2). Staining experiments revealed lipids in the pericarp (Figure 3), and the removal of pericarp confirmed that its presence facilitates caryopsis removal by ants. In other species of *Setaria*, alternative seed dispersal modes such as epizoochory have been reported (Carlquist & Pauly, 1985). In contrast, in *S. viridis*, mature seeds detach completely from the panicle and fall to the ground, and the long awns are unable to adhere to animal fur (personal observation, A.Y.). These results indicate that the pericarp functions as an elaiosome in *S. viridis*, suggesting that this species is a typical myrmecochorous plant in Japan. Several studies have reported the presence of elaiosomes in Poaceae genera including *Chasechloa*, *Echinolaena*, *Hildaea*, *Ichnanthus*, *Oedochloa*, and *Yakirra* (Berg, 1985; Davidse, 1987; Silva et al., 2015, 2017) and have suggested that elaiosomes promote seed removal by ants (Berg, 1985). To the best of our knowledge, this study provides the first experimental evidence of myrmecochory in the Poaceae, incorporating observations of ant behavior, seed fate, and the chemical characteristic of the elaiosome.

The caryopses of *S. faberi* were also dispersed by ants, but at a lower frequency. The low seed removal rate suggests that this species either has smaller elaiosomes than those of *S. viridis* or that its elaiosome compounds are less attractive to ants. Moreover, *T. tsushimae* did not consume the pericarp of the *S. faberi* caryopses (Figure 2). Because *S. faberi* is closely related to *S. viridis* (Kim et al., 2015), this may suggest an intermediate step in the evolution or loss of ant–seed dispersal. Future studies are needed to quantify the lipid content of elaiosomes and to examine a broader range of populations.

Tetramorium tsushimae is a well-known seed disperser of many plant species, including *Lamium amplexicaule* (Lamiaceae) (Tanaka et al., 2015), *Thesium*

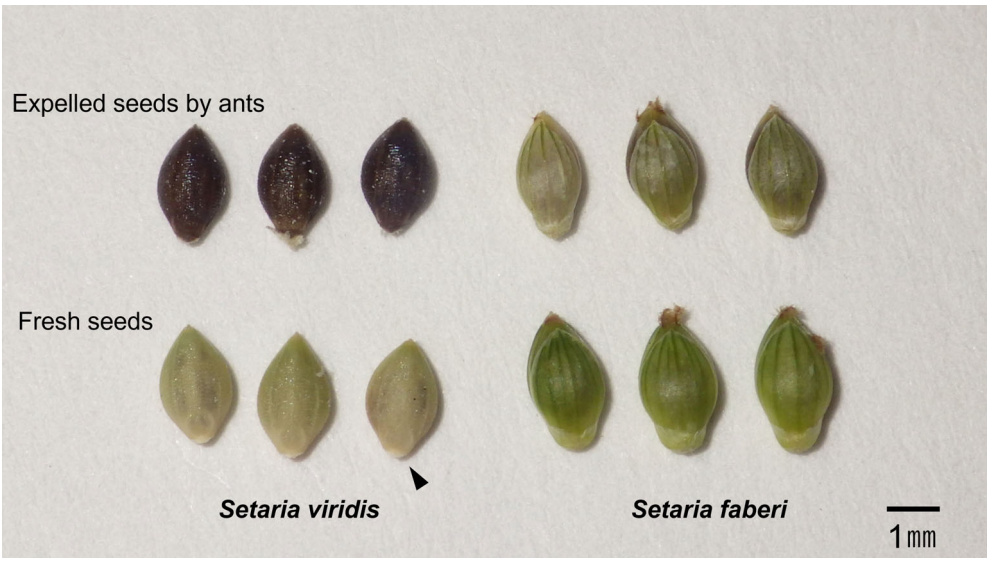


FIGURE 2 Seeds of *Setaria viridis* and *Setaria faberi*. Top row, seeds that have been expelled from a nest of *Tetramorium tsushimae*. Bottom row, fresh seeds that have fallen from the spikes. Black arrowhead, location where lipids were detected by Sudan IV stain.

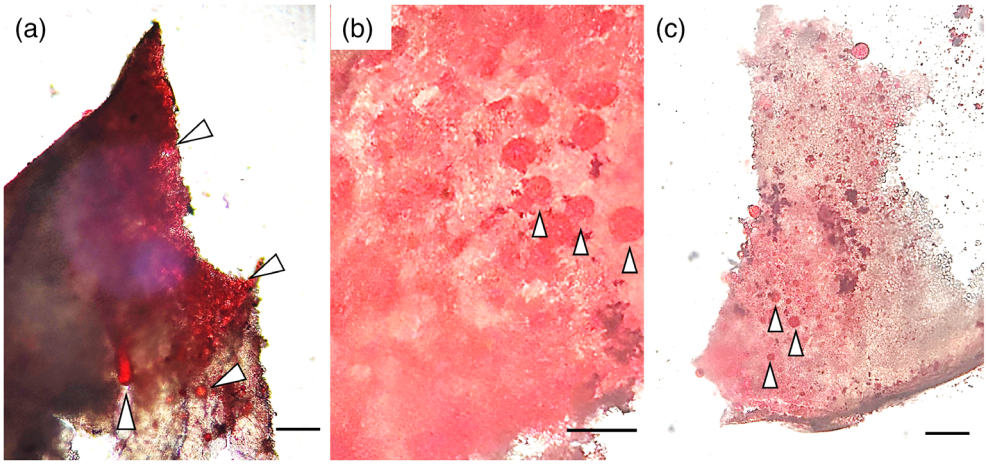


FIGURE 3 Photomicrographs of transverse sections of the pericarp of (a, b) *Setaria viridis* and (c) *Setaria faberi*, stained with Sudan IV, showing cells impregnated with lipophilic material (arrowheads). Scale bars = 100 μm (a, c); 20 μm (b).

chinense (Santalaceae) (Suetsugu, 2015), *Oenothera biennis* (Onagraceae) (Ohtsuka et al., 2020), and *Sporobolus fertilis* (Poaceae) (Steud.) Clayton (Ohtsuka et al., 2020) in Japan. The mean seed dispersal distance identified here was ~38 cm, which may reduce sibling competition compared with the highly localized dispersal by gravity. In addition, in some cases, the transport of seeds by *T. tsushimae* to their nest helps to protect dispersed seeds from predators, such as stinkbugs (Tanaka et al., 2015). The seeds of *S. viridis* and *S. faberi* are also consumed by the earthworm *Pheretima guillelmi* (Kinberg) (H. Li, Jiang, et al., 2020) and by ground beetles (Heggenstaller et al., 2006). Seed dispersal by *T. tsushimae* may contribute to protection from these predators.

The genetic diversity of *S. viridis* has been studied globally, as it is an emerging model species (Dekker, 2004; Huang et al., 2014). In Japan, the coastal populations of *S. viridis* are usually assigned to a separate variety, *S. viridis* var. *pachystachys* (Franch et Savat.) Makino et Nemoto, which has been documented in coastal habitats of East Asia, including Japan and southern China (Itoh et al., 2024; Osada, 1989). This variety most likely evolved from *S. viridis* (Kim et al., 2015). Moreover, *S. viridis* often exhibits dwarf morphology with short panicles and reduced height in urban areas (Figure 4), where it is often found adjacent to nests of *T. tsushimae*. These ants may facilitate seed dispersal in the limited soil available in cities. Seed dispersal by ants may support the establishment of *S. viridis* populations in coastal habitats or urban areas and contribute to local adaptation and diversification. Future research should focus on variations in the dependence of seed dispersal mutualism on the local adaptation of *S. viridis* to further explain the role of seed dispersal mutualism in plant diversification.

In addition, our findings provide a model system for the genomic study of plant–ant seed dispersal mutualism. Model systems have been constructed for pollination, root nodule, and mycorrhizal symbioses (Kamel et al., 2017; M. Li et al., 2019; T. Li, Fan, et al., 2020),

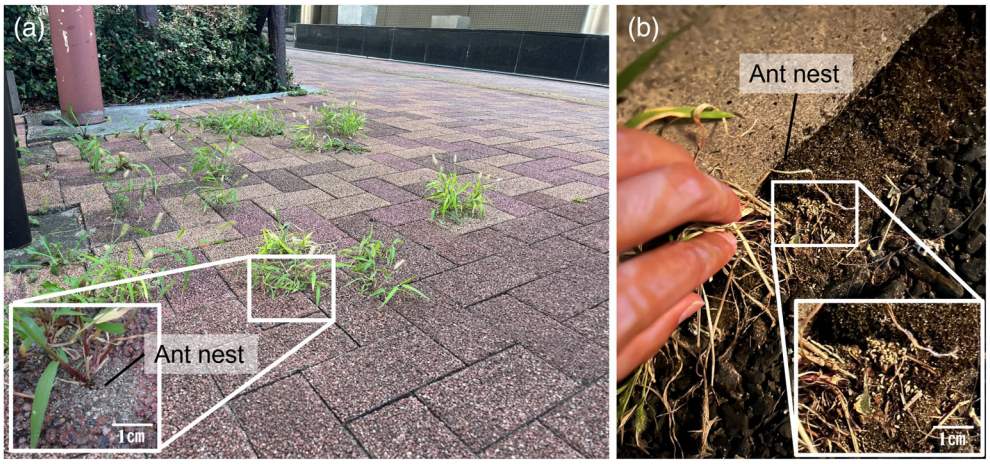


FIGURE 4 (a) *Setaria viridis* growing in the city. (b) Seeds of *S. viridis* around nest entrance of *Tetramorium tsushimae*.

advancing the understanding of these mutualisms. Genomic resources for *S. viridis* have been provided by Mamidi et al. (2020), and numerous mutants have been developed and maintained at various research institutes (Brutnell et al., 2015). The identification of *S. viridis* as a model plant for seed dispersal mutualism opens a new field of genomic research on plant–animal mutualism.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request. [Correction added on 16 January 2026, after first online publication: The Data Availability Statement was changed.]

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